Title

Heterogeneous individuals impede the establishment of cultures in animal groups

Andrew T. L. Allan[1,2,3*], Guy Cowlishaw[2], Simon Kenworthy[2,3], & Alecia J. Carter[3]

[1] Department of Anthropology, Durham University, Durham, U.K

[2] The Institute of Zoology, Zoological Society of London, Regent's Park, London, UK

[3] Department of Anthropology, University College London, London, U.K.

*Corresponding author: andrew.allan@durham.ac.uk

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Abstract

Social learning facilitates the diffusion of novel behaviours (i.e., inventions) through groups and is a key component in the development of culture. The speed with which an invention spreads through a group is largely determined by the strength of social connections and network structure; however, research concerning the establishment of inventions (i.e., culture) has typically overlooked that individuals differ in their propensities for social learning. The aim of this study was to assess how the presence and extent of heterogeneity in propensity for social learning can interact with transmission probability (i.e., the complexity and regularity of the task being performed), network size and structure, and attribute distributions (i.e., homophilic or random) to regulate the likelihood of establishing inventions. We found that the extent of information diffusion was lower in heterogeneous than homogeneous populations, but only when transmission probability was at intermediate levels – full adoption of an invention in a group was consistently observed when transmission probability was high (e.g., simple, regularly occurring tasks) but was rare when transmission probability was low (e.g., complex and rarely occurring tasks). When heterogeneity was held high, homophilic distributions had an additional negative effect on the extent of information diffusion, but again, only when transmission probability was at intermediate levels. Given the variety of intraspecies phenotypic diversity identified in wild animals, our results highlight the importance of including heterogeneity and homophily when investigating culture. Researchers can use our model to make predictions about the conditions that may facilitate animal culture in a wide range of taxa.

Introduction

Individuals can acquire information either personally via interacting directly with their environment, or socially, via observing the behaviour of or products made by other individuals (Dall et al. 2005). Acquiring personal information can require time, which can be costly to individuals who also need to engage in other fitness enhancing tasks, and can involve costly mistakes (Templeton and Giraldeau 1996; Laland 2004). Social animals can alleviate these costs by acquiring information and learning from their social partners. However, social information can become rapidly outdated (Carter et al. 2016).

Despite its potential costs, social learning is the foundation of animals' second inheritance system: inheritance of behaviours via observational learning (Whiten 2017). Because social learning is essential for the diffusion of novel information between individuals and through groups (Duboscq et al. 2016), its role in the development of cultures and traditions within species has garnered considerable research attention (Castro and Toro 2004; Schuppli and van Schaik 2019). While culture has been defined in many ways (Perry 2006), there is universal agreement that it is reliant upon the transmission of inventions (i.e., novel behaviours) amongst individuals, regardless of the precise social learning mechanism used (Schuppli and van Schaik 2019).

For a behaviour to become adopted as a cultural trait (i.e., innovation) there is a three-step process: (1) invention – the creation of a novel behaviour; (2) transmission – the behaviour must spread through individuals or groups via a social learning; and (3) establishment – the behaviour or trait must spread widely through the group and be maintained across generations via social learning (Perry et al. 2021). Experimental and observational research have shown that age, sex, social network position, and personality can have key roles in determining the first step - an individual’s propensity to invent (Perry et al. 2021). Theoretical and empirical research have shown that social network structure and the strength of social connections are key regulators of the second step – transmission (Christensen, Albert, Grenfell, & Albert, 2010; Griffin & Nunn, 2012; Guimarães et al., 2007; Pastor-Satorras & Vespignani, 2001; Salathé & Jones, 2012). Additionally, both the individuals demonstrating and learning social information can demonstrate among-individual differences that affect transmission processes (Laland 2004; Perry et al. 2021). For example, the adoption of a novel behaviour by a naïve individual into their behavioural repertoire can depend on the demonstrator’s rank (Kendal et al. 2015; Canteloup et al. 2021), sex (van de Waal et al. 2010), and age (Duffy et al. 2009). Likewise, a learner’s age (Thornton and Malapert 2009), sex (Aplin et al. 2013), rank (Kendal et al. 2015), and personality (Carter et al. 2014) can determine whether they learn and thus adopt a novel behaviour.

The patterning of social relationships in a network also has a strong influence on determining whether cultural traits establish (i.e., the third step – inventions becoming fully adopted and maintained as a stable characteristic of a group via social learning) (Perry et al. 2021). For example, in denser networks, individuals can interact more frequently, promoting social learning (Lerman and Ghosh 2010). Modular networks can ‘trap’ novel information among clusters of individuals (Weng et al. 2013), thus reducing the likelihood of cultures emerging (Perry et al. 2021). However, other than social position, research has typically overlooked the role that other forms of individual heterogeneity (i.e., phenotypic differences) may play in the establishment step of animal cultures (Reader and Laland 2000; Mann and Singh 2015; Evans et al. 2021; Perry et al. 2021), despite these among-individual differences proving to be important in the invention and transmission steps (Laland 2004; Perry et al. 2021).

The role of individual heterogeneity in the emergence of animal cultures is complicated by a host of additional factors that determine how likely it is for social learning to take place successfully, i.e., the ‘transmission probability’. These factors include behavioural complexity (e.g., one-step vs multi-step tasks), spatially/temporally contingent tasks (e.g., termite fishing), and network characteristics (e.g., size, efficiency, modularity, etc). In the first case, behaviour or task complexity in foraging contexts could derive from the number of processing steps an individual is required to make to access a food item. Individuals may succeed at learning one-step foraging tasks socially but fail to solve two-step tasks despite having access to social information (van de Waal and Bshary 2011; van de Waal et al. 2013). In non-foraging scenarios, complexity may be derived by individuals needing to learn to perform behaviours correctly in the correct context. For example, juvenile chimpanzees (*Pan troglodytes*) learn rank-related gestures for submission and appeasement scenarios (Scott 2013; Bard et al. 2014), whilst referential (i.e., predator specific) call associations can depend on age and experience with predators, even if individuals display one-trial social learning of call functions (Deshpande et al. 2022).

In the second case, transmission probability may also depend on whether the behaviour is spatially/temporally contingent. For example, termite fishing by chimpanzees (Lonsdorf 2005) and predation on young antelopes by baboons (Strum 1975; Allan et al. 2022) both concern spatially rare resources whose abundance varies seasonally. Despite the clear role that behavioural complexity and spatial/temporal dependency play in social learning processes, little research has explored how these factors interact with individual heterogeneity to determine whether novel behaviours become established within animal groups. It seems likely that with very simple/frequently performed or very complex/less frequently performed behaviours, the role of individual heterogeneity may be minimal as groups either learn rapidly (i.e., easy and frequently observed behaviours) or cease social learning entirely (i.e., very complex and infrequently observed behaviours). Thus, the effect of individual heterogeneity is likely to be maximised when behavioural complexity and spatial/temporal dependency are at intermediate levels. However, it remains unclear whether we would predict a positive or negative effect of individual heterogeneity on the likelihood of novel behaviours establishing at these intermediate transmission probabilities.

In the third case, the effects of network size and structure may also interact with individual heterogeneity to determine the likelihood of novel behaviours establishing. Typically, research investigating the role of network structure on diffusion performance has focused on degree distribution (i.e., the fraction of nodes in a network with *k* connections to others nodes) (Newman 2002; Jackson and López-Pintado 2013), with greater diversity in the number/strength of social bonds and distance between nodes leading to a reduction in the speed, fidelity, and robustness of information diffusion (Voelkl and Noë 2010). Networks exhibiting higher clustering coefficients (i.e., tendency for nodes in a network to cluster together) and lower robustness (i.e., the capacity of the network to maintain functionality when nodes are sequentially removed) can limit the extent of diffusion compared to networks exhibiting greater robustness and lower clustering coefficients, implying that highly clustered networks may trap or bottleneck information amongst highly connected nodes (Naug 2008). However, research into animal cultures has yet to explore whether the presence and extent of heterogeneity has differential effects on the likelihood of novel behaviours successfully establishing in networks with varying characteristics (e.g., size, density, modularity).

In addition to individual heterogeneity, how those individuals are distributed in animal networks may affect the likelihood of cultures emerging. In particular, whether social learners are connected to other social learners (positive assortment, or homophily) or others less likely to collect and use social information (negative assortment, or heterophily) may affect information diffusion through groups (Pinter-Wollman et al. 2011; Carter et al. 2015; Hasenjager and Dugatkin 2017). While homophily may promote initial diffusion of information through local clusters of individuals with a high propensity for social learning (Guilbeault et al. 2018), it may hinder the spread of an invention across an entire group, and thus, decrease the likelihood of novel behaviours establishing (i.e., emergence of culture).

The aim of this study was to assess the extent to which heterogeneity in social learners affects the likelihood of inventions becoming established. We explored this question across a range of transmission probabilities and through observed animal networks exhibiting different structures. To facilitate this research, we used agent-based modelling (ABM) as it is a powerful tool for modelling diffusion processes and allows for learners' traits to be considered in social learning interactions. We specifically investigated the following four questions: (i) Does the presence and extent of heterogeneity amongst individuals' propensities for social learning interact with transmission probability (e.g., task complexity) to influence the likelihood of inventions establishing? (ii) Are some networks more robust to heterogeneity than others? (iii) Does the extent of heterogeneity interact with network size and structure to affect the likelihood of inventions establishing? And (iv) Does homophily according to propensity for social learning affect the likelihood of inventions establishing?

Model description

Model purpose

The model was implemented in NetLogo (version 6.1.1) and aimed to assess the effect of heterogeneity of learners on the likelihood of an invention becoming established (i.e., fully adopted) in static animal networks obtained from open-source data repositories. We systematically varied the transmission probability and attribute distribution (i.e., random or homophilic distributions) of agent's propensities for social learning to determine their influence on the likelihood of novel behaviours becoming established. Agents could only learn socially; thus our model did not allow for personal (i.e., asocial) learning. This decision was made as we wished to focus exclusively on the social learning mechanisms governing the development of animal cultures. Below we describe the model following the ODD paradigm (Grimm et al. 2006).

State variables and scales

The model comprised two levels: individual and population. The population (i.e., animal network) was loaded from matrices stored on the host computer in a distinct command to the 'go' procedure (that initiated social learning). Animal networks were derived from published research on five different species that we were able to source through online repositories (e.g., Dryad, blog.datadryad.org) or datasets included as supplementary material in published papers (Fig 1). These included: (1) a remotely-collected raccoon (*Procyon lotor*) contact network of 22 individuals (Reynolds et al. 2015), (2) a remotely-collected domestic dog (*Canis familiaris*) contact network of 48 individuals (Wilson-Aggarwal et al. 2019), (3) a directly-observed baboon (*Papio ursinus*) grooming network of 58 individuals (Carter and

Cowlishaw 2021), (4) a remotely-collected sleepy lizard (*Tiliqua rugosa*) contact network of 60 individuals (Bull et al. 2012), and (5) a remotely-collected network of co-occurrence at feeders of 82 individuals of mixed bird species (blue tits *Cyanistes caeruleus*, great tits *Parus major* and marsh tits *Poecile palustris*) (Farine et al. 2015). Due to differences in data collection methods across studies we binarized all networks, such that all connections were coded as 1 regardless of connection strength and 0 if individuals were not associated. As such, 'strength' of social connection played no part in our social learning procedure.

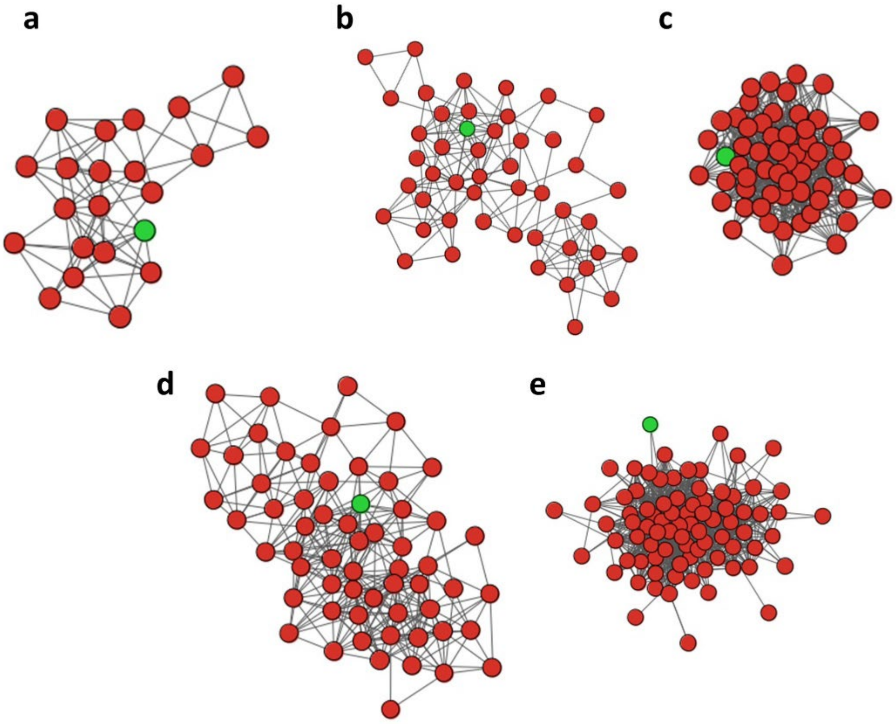

Fig 1. The networks diagrams of the five different species we explored. The top-left panel is the (a) raccoon network (22 individuals), (b) dog network (48), (c) baboon grooming network (58), (d) sleepy lizard network (60), and (e) mixed bird species network (82). Node colour indicates the state of the individual (naïve = red, informed = green). At the beginning of a simulation, only one individual, the seed, was informed.

Individuals were assigned a single characteristic (*propensity to learn socially*) and could be in one of two knowledge states (naïve or informed). The *propensity to learn socially* value captured variance in and represented individuals' abilities to acquire knowledge of the invention and successfully exploit this knowledge to gain a benefit, thus allowing them to transmit that information to others (Carter et al. 2016). The model did not distinguish between individuals who were naïve *sensu stricto* (i.e., they had not learned the solution to a task) and those that were 'naïve' in practice (i.e., learned the invention but fail to apply the information correctly and are thus unable to act as demonstrators), as neither can pass information on to others (Carter et al. 2016).

Two further population variables in our model governed the scale of the values assigned to individuals for their propensity for social learning: *propensity to learn socially mean,* L_{mean}, and *propensity to learn socially range,* L_{range}. L_{mean} determined the average ability of the population to learn socially, whilst L_{range} determined the population's heterogeneity in *propensity to learn socially* values around L_{mean}. An individual's *propensity to learn socially*, L_{ind}, was calculated as L_{mean} plus a number drawn randomly from a normal distribution with a mean of 0 and standard deviation set by the value of L_{range}. As such, higher L_{range} resulted in greater heterogeneity in a population's propensity to learn socially. We also included an individual-level variable, P_{ind}, to represent the prestige of the demonstrator (i.e., social learning should be more likely when demonstrators have higher prestige/share stronger bonds with the learner), however we did not systematically alter the value of this variable in the simulations for this study.

We also included an individual-level variable to capture stochastic processes: *random stochasticity.* This was included as social learning may not always occur, even if the context and scenarios predict that it should (e.g., a naïve individual with a high propensity to learn may fail to learn from a high prestige demonstrator). Individuals may fail to learn despite being given the opportunity to acquire social information (Carter et al. 2016; Perry et al. 2021), whilst demonstrators may not always share their knowledge, i.e., voluntary inhibition

(Drea and Wallen 1999; Carter et al. 2014). Given that individuals with a higher tendency to monitor others may also learn and adopt new behaviours sooner (Lonsdorf 2005), the likelihood of social learning taking place should also depend on whether learners are attentive and facing the right direction at the right moment in time; however, this source of stochasticity has yet to be quantified in any study system.

At the network level, we also included the variable *transmission probability* (*TP*), which captured how likely a task was to be transmitted between an informed and naïve individual, independent of the characteristics of the individual learners. Given that P_{ind} was held constant to reduce the number of factors tested in this study, *TP* therefore encapsulated variability relating to the characteristics of the demonstrator (e.g., prestige), the strength of social bonds between learners and demonstrators, plus the complexity and spatial/temporal dependency of the behaviour being transmitted. Low values of transmission probability could therefore reflect difficult-to-learn behaviours that require more attention to learn such as a multi-step process, an infrequently performed behaviour such as a foraging technique only applied to spatially rare food items (e.g., termite fishing), or instances where informed demonstrators have low prestige (e.g., juveniles) such that learners may be less likely to collect social information from them.

Initialization

The distribution of values assigned to individuals for their *propensity to learn socially*, L_{ind}, was distributed randomly or assorted such that individuals with similar propensities for social learning shared direct connections (i.e., homophily). Values for *Propensity to learn socially* were assigned to individuals by a distinct command embedded within the procedure for loading animal networks from the host computer, and thus, were completed before the 'go' procedure was initiated that initiated social learning in the group (see *Process overview and scheduling*).

We employed three distinct processes for generating attribute distributions, (1) random (no types), (2) random (with types), and (3) homophilic (with types). When 'random (no types)' was used, each individual's propensity for social learning values, L_{ind}, were calculated as L_{mean} plus a number drawn randomly from the normal distribution (mean = 0 and standard deviation = L_{range}). This calculation resulted in a random distribution of L_{ind} across each network (i.e., assortativity was close to zero, see table S1).

To produce homophilic allocations of L_{ind} we adapted the code for producing homophilic distributions from (Kapeller et al. 2019) by creating three types of agents: low (LPL), medium (MPL), and high propensity to learn (HPL). Initially, the whole population were categorised as MPL and two individuals were randomly selected, one to be LPL, and the other one to be HPL. The link neighbours of the LPL and HPL individuals were then identified as 'pools' of potential LPL or HPL individuals. We used a sequence of loop commands and in each step an MPL individual from each pool of potential LPL and HPL individuals was selected and transformed into LPL and HPL 'types' respectively. This process was repeated until a 40:30:30 ratio for MPL:LPL:HPL proportions was reached, as this generally followed a normal distribution (see fig 1, panels b, d, f, h, and j). In cases where one type hindered the spread of another type such that the 40:30:30 ratio could not be achieved, the procedure was cancelled and the population reverted to MPL type, and the initial LPL and HPL individuals re-selected.

As we wished to compare diffusion performance between random and homophilic allocations for part of our analyses, we also generated random allocations using these behavioural 'types'. When using 'random (with types)' the individuals were randomly selected to be one of the three types according to the 40:30:30 ratio (see fig 2, panels a, c, and e). When using homophilic (with types) or random (with types) attribute distributions the LPLs were assigned an L_{mean} of 35, MPLs assigned an L_{mean} of 50, and HPLs assigned an L_{mean} of 65. L_{range} was set to 10 in all cases as homophily is only possible with variation in the attribute of interest. In both cases the L_{mean} and L_{range} for the population was the same, but the assortative coefficient (Farine 2014) was noticeably higher than zero for homophilic allocations (see table S1), indicative of homophily according to *propensity to learn socially*, and close to 0 for all networks when random (with types) was chosen.

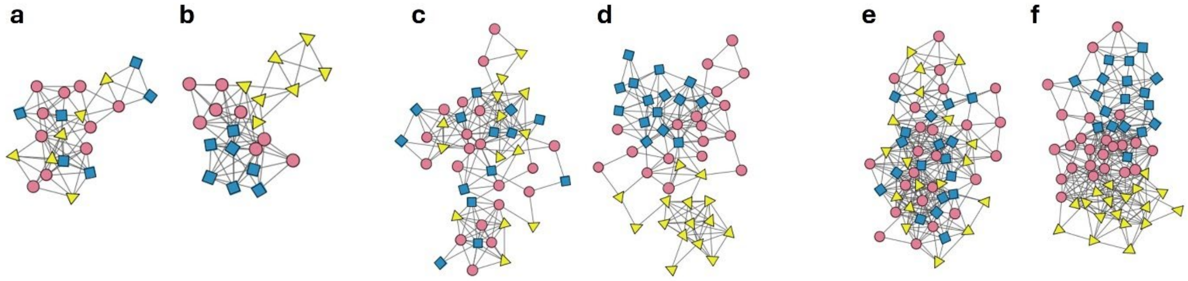

Fig 2. Example network diagrams exhibiting different attribute distributions. Shown are the (a, b) raccoon, (c, d) dog, and (e, f) sleepy lizard networks with (a, c, e) a random attribute distribution and (b, d, f) the same networks with a homophilic distribution. Node colour/shape indicates the state or 'type' of the individual, LPL (low propensity to learn) = yellow/triangle, MPL (mid propensity to learn) = pink/circle, and HPL (high propensity to learn) = blue/square.

Each time a network and attribute distribution was generated, a single individual was selected at random to begin in an 'informed' state (i.e., the seed), whilst the remaining individuals were 'naïve' to the new behaviour (see fig 1).

Process overview and scheduling

The individuals in the model were static. The model proceeded in time steps that represented learning 'bouts', in which individuals could only interact with (i.e., pay attention to and learn from) another individual with whom they shared a direct network connection. The only scale variable was time steps (ticks), with the tick counter increasing by one once the following conditions were met: i) all naïve individuals in the network had paid attention to one of their neighbours (i.e., a direct linked agent in the network), and ii) attempted to learn from the neighbour they were 'paying attention' to. Learning could only occur if the neighbour (i.e., demonstrator) had already adopted the new behaviour, refer to the *transmission process* section for further details. We set the step-horizon (i.e., maximum number of steps before the model was forced to end) to 5000 steps.

Transmission process

In all models, at each step, all naïve actors followed the same 5-step transmission process to determine whether they would become informed:

(i) Select randomly a linked neighbour to pay attention to.

(ii) If the linked neighbour was not 'informed' then the actor remained naïve and exited the process.

(iii) If the linked neighbour was informed, the following calculation was made:

$$\text{Naïve individual's } L_{ind} + \text{Informed demonstrator's } P_{ind} + RS > 100 - TP$$

To keep the left-hand side of the equation proportional to the right-hand side, we converted L_{ind}, P_{ind}, and RS to proportions using a common denominator and then multiplied their sum by 100. The denominator was the sum of the maximum values of L_{ind} and P_{ind} exhibited by the agents (always 50 in the case of P_{ind}), and the upper bound of *RS*. This ensured each variable was given equal weighting in the learning process. *RS* was therefore a key determinant in the learning process and encapsulated real-world scenarios whereby naïve individuals may not be paying close attention to demonstrators at the right moment in time.

(iv) If calculation (iii) was false, then the actor remained naïve and exited the process.

(v) If calculation (iii) was true, then the actor passed to a final procedure where a random floating-point number between 0 and 100 was generated (thus scaling the equation in the 0-100 interval). If this number was less than the *TP*, then the individual would learn/adopt the new behaviour and thus update their status to informed. Otherwise, the individual would remain naïve and cease paying attention to their informed neighbour.

End-of-run

Once the transmission process was completed within a single step, the step counter (number of ticks elapsed) would advance by 1. The transmission process was repeated amongst uninformed individuals until either the whole population became informed, or the maximum number of steps (5000) was reached.

Simulation submodels

To explore the effect of heterogeneity on the establishment of inventions (i.e., full adoption of new behaviours), we created separate submodels for each animal network, transmission probability, and L_{range}. Submodels were simulated in *BehaviorSpace* for each combination of values/settings listed in table 1. Specifically, we held L_{mean} and P_{ind} constant but varied L_{range} (0, 5, or 10), the network type (figs 1), and the transmission probability (5%–50% in 5% increments). We also held the ‘prestige’ of the ‘informed’ demonstrator constant at 50, but included an option in the model for this to be altered by researchers in future work. This produced 150 submodels (30 for each animal network) which were run for 50 repetitions each, resulting in 7,500 total runs. From these simulations we extracted the network metrics for each animal network at each value of N_{ind}. These included network density, the mean and average clustering coefficients (Wilensky 2021), global efficiency (Pasquaretta et al. 2014), and the continuous assortative coefficient (Farine 2014), the values of which are summarised in table S1.

Table 1. Model parameters, their description, and values for simulations in *BehaviorSpace* for all models using random attribute distributions for propensity to learn.

Level	Parameter	Description	Values
Individual	L_{ind}	An individual’s propensity to learn socially	Determined by L_{mean} and L_{range}
Individual	P_{ind}	An informed demonstrator’s prestige	50 (held constant for all individuals)
Population	L_{mean}	Mean propensity to learn socially for all individuals	50
Population	L_{range}	Heterogeneity in propensity to learn socially	0, 5, 10
Individual	*RS*	Random stochasticity, each individual generated a random floating-point number between 0 and the value of *RS.*	50

Population	*TP*	Transmission probability	5, 10, 15, 20, 25, 30, 35, 40, 45, 50

To explore the effect of attribute distributions on the establishment of inventions, we created further submodels for each network, explicitly varying transmission probability and allocation (random with ‘types’ or homophilic). We held the same variables constant as mentioned previously but additionally held L_{range} at 10 to maximise individual heterogeneity across random and homophilic allocations. Submodels were again simulated in *BehaviorSpace* for each combination of values/settings. This produced 100 submodels (20 for each animal network) which were run for 50 repetitions each, resulting in 5,000 total runs. We calculated the same network metrics as with heterogeneity submodels (see table S1).

We measured our response variable at the end of each run of each submodel - the proportion of the network informed by 5000-time steps (i.e., the extent of information diffusion). We also calculated the number of time steps until every group member was informed (i.e., complete adoption) and provide figures of these results in supporting information (see figures S1 and S2).

Statistical analysis

It is considered inappropriate to analyse simulation data from agent-based models using statistical inference (e.g., rejecting a null hypothesis via P-value estimation) (von Brömssen and Röös 2020; Ekanayake-Weber and Swedell 2021). The two key issues with such an approach are (1) the modeller would be testing null hypotheses they know a-priori to be false, and (2) the statistical power is determined (and can be inflated) by the number of simulations the modeller elects to run (White et al. 2014). As a result of these issues, it is advised instead to quantify the magnitude of effect sizes using descriptive statistics (White et al. 2014). This approach is typically used to compare effect sizes among the descriptive statistics of simulated data versus real-world data (Hoban et al. 2012; von Brömssen and Röös 2020; Ekanayake-Weber and Swedell 2021); however, we implement the approach here to compare the effect sizes among descriptive statistics (of diffusion performance) between networks varying in population size and structure. As such, our analysis compared the consistency of diffusion performances (proportion of the network informed by 5000 time-steps) across multiple simulation runs using the median and upper/lower quartile for diffusion performance across 50 simulations.

For the first part of our analysis, we explored the question: Does the presence and extent of heterogeneity (in propensity for social learning) interact with transmission probability to influence the likelihood that an invention becomes established (i.e., a novel behaviour becomes full adopted) in each animal network? We compared the effect sizes of diffusion outcomes (i.e., proportion of the group that adopted the invention) produced by each propensity to learn (socially) variation value (i.e., L_{range} = 0, 5, or 10) across the *Transmission Probability* range (5 – 50% in 5% increments) in each animal network. Given that each network exhibited a different number of individuals (i.e., nodes) and varying network characteristics (e.g., density, mean clustering coefficient), these analyses also addressed whether these network factors may interact with the extent of individual heterogeneity to affect the likelihood of inventions establishing. For these analyses, we used the simulation data with random attribute distributions (no types).

For the second part of our analysis, we explored the question: Does homophily according to propensity for social learning affect the likelihood that an invention becomes established? For this analysis we compared the effect sizes of diffusion performance produced by different attribute distributions (of *propensity to learn socially* values) across the *Transmission Probability* spectrum and across each animal network. *Attribute Distribution* was either random or homophilic, with each derived from their respective simulation data – random attribute distribution (with types) or homophilic attribute distribution (with types).

Results

When heterogeneity was held at zero (i.e., homogeneity), all animal networks consistently approached full adoption (i.e., establishment of an invention) once transmission probability was 15% or higher (fig 3), whilst moderately and highly heterogeneous networks did not consistently reach full adoption until 20% and 25% respectively. The only exception was the raccoon network (the smallest network, see fig 3) where homogeneous individuals consistently reached full adoption at 10% transmission probability, but otherwise produced identical patterns to the other networks. Given that these networks varied in size (i.e., number of individuals) and characteristics (i.e., network density, the mean and average clustering coefficients, and global efficiency - see Table S1), our results demonstrate that the presence and strength of individual heterogeneity can have overarching effects that hinder the establishment of an invention.

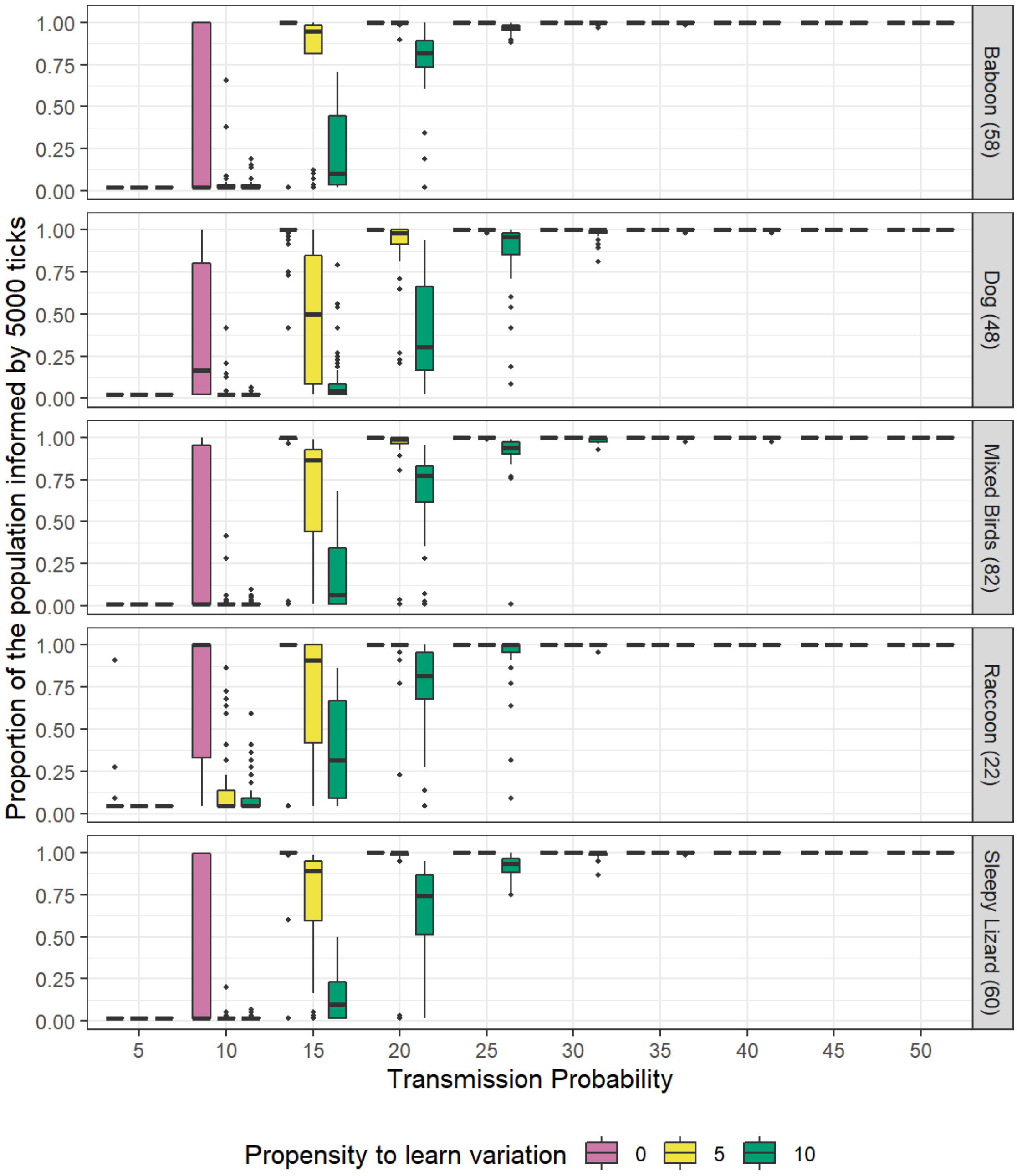

Fig 3. Boxplots showing the proportion of individuals informed by 5000 ticks (i.e., the diffusion performance) at various levels of transmission probability (5% to 50% in 5% increments) for observed networks. Boxplots show 25% and 75% quartiles (boxes), median (bold line within boxes), 1.5 x the respective inter-quartile ranges (whiskers), and outlying points (black dots) for the diffusion performance across the 50 simulations in each context. Each coloured box represents various values for *propensity to learn socially* variation (0, 5, and 10), the pink, yellow, and green boxes therefore refer to homogeneous, moderately heterogeneous, and highly heterogeneous networks respectively. Each panel is a different *species* (baboon grooming, dog, mixed birds, raccoon, sleepy lizard); numbers in parentheses represent the population size for each network. *Propensity to learn socially* mean and the maximum *Random stochasticity* were held constant at 50% to ensure equal weighting when summed against *Transmission Probability.*

When variation in *propensity to learn socially* was held constant at 10 (i.e., high individual heterogeneity), we found that greater proportions of animal groups adopted an invention with random than homophilic distributions (i.e., the median proportion of individuals adopting the invention in random distributions was approximately equal to or higher than the 75% quantile of homophilic allocations), but only when transmission probability was in the 20-30% range (see fig 4). Outside of this range, when inventions were either challenging (i.e., transmission probability < 20%) or simple to learn (i.e., transmission probability > 30%), we detected no effect of attribute distribution on the likelihood of an invention establishing in any animal group.

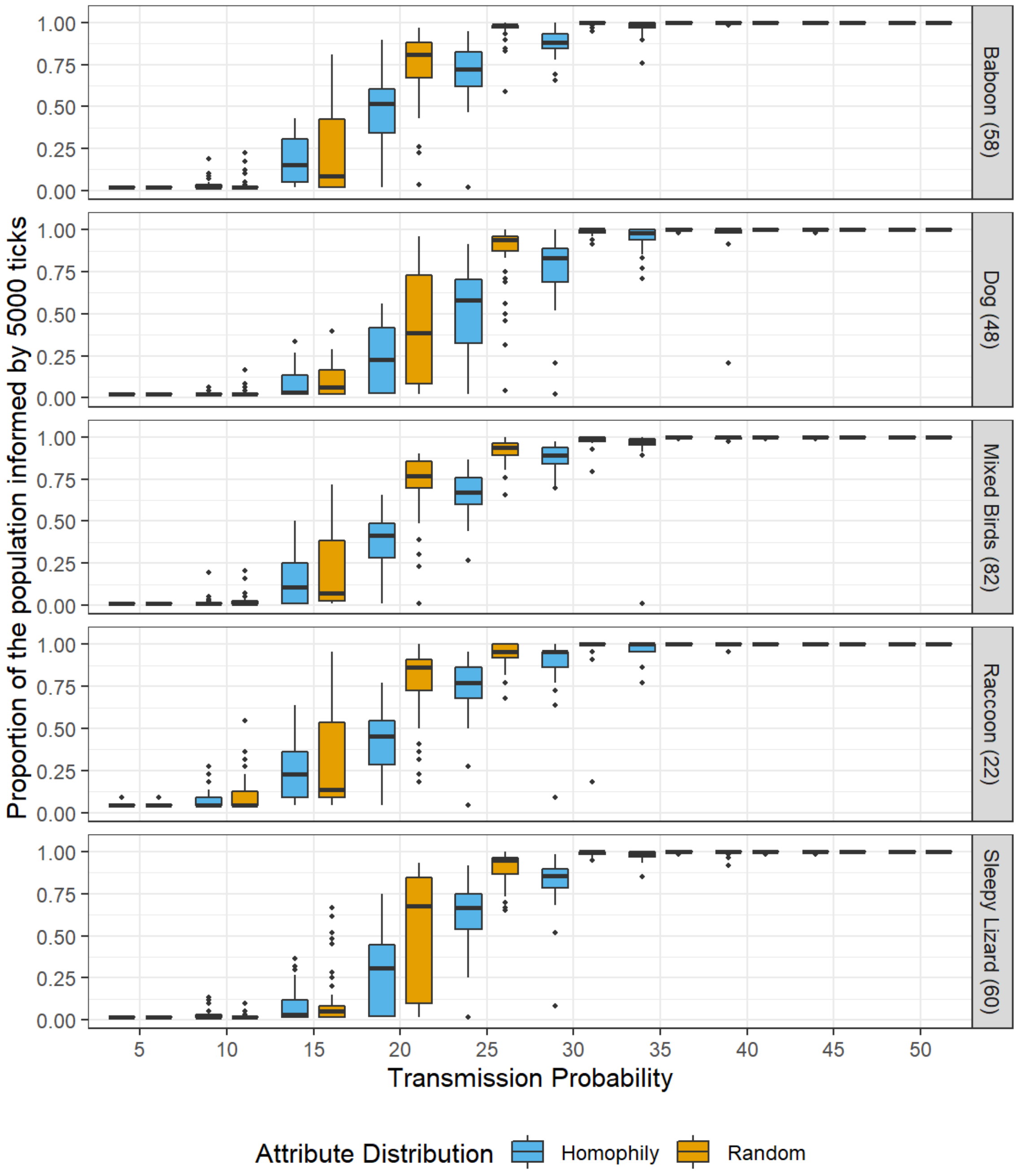

Fig 5. Boxplots showing the proportion of individuals informed by 5000 ticks (i.e., the diffusion performance) at various levels of transmission probability (5% to 50% in 5% increments) for observed networks. Boxplots show 25% and 75% quartiles (boxes), median (bold line within boxes), 1.5 x the respective inter-quartile ranges (whiskers), and outlying points (black dots) for the diffusion performance across the 50 simulations in each context. Each coloured box represents the *attribute distribution* for *propensity to learn socially* (blue – homophilic, orange - random) and each panel is a different *species* (baboon grooming, dog, mixed birds, raccoon, sleepy lizard), numbers in parentheses represent the population size for each network. *Propensity to learn socially* mean and the maximum *Random stochasticity* were held constant at 50% to ensure equal weighting when summed against *Transmission Probability.*

Discussion

The emergence of animal culture has three steps: firstly, a novel behaviour must be created (i.e., invention); secondly, the new behaviour must be adopted by other individuals via social learning (i.e., transmission); and finally, the invention must spread and be maintained as a stable characteristic of the group by social learning mechanisms (i.e., establishment) (Schuppli and van Schaik 2019). Research has shown that there is variation in the likelihood and rate of learners adopting an invention, either due to varying opportunities to access social information (Aplin et al. 2012; Carter et al. 2016) or due to the varied characteristics of the learners and demonstrators involved (Carter and Cowlishaw 2021). Despite research demonstrating numerous sources of heterogeneity in both the individuals providing information and those acquiring social information (Laland 2004; Perry et al. 2021), theoretical models exploring the factors governing the establishment of inventions have generally assumed that individuals within networks are homogeneous in their traits (Reader and Laland 2000; Evans et al. 2021), and thus equally likely to acquire or share social information. In this study we developed an agent-based model to assess the extent to which heterogeneity in learners and homophily according to propensity for social learning influenced the likelihood of inventions establishing. We found that both heterogeneity and homophily had negative effects on the likelihood of populations fully adopting an invention but only when the transmission probability was within certain ranges.

Increasing learner heterogeneity inhibited the diffusion process, which was assessed by comparing the proportion of the population informed by 5000 time-steps. Homogeneous populations often achieved full adoption of the invention even when transmission probability was relatively low, whilst highly heterogeneous populations did not achieve full adoption until transmission probability was relatively high. These results demonstrate that overlooking individual heterogeneity can produce anticonservative estimates concerning the outcomes of diffusion processes, potentially misleading our understanding of the factors regulating the emergence of animal cultures.

By adopting an agent-based modelling approach, our model was able to use a single variable (i.e., propensity to learn socially) that encapsulated any individual-level factors that could influence the likelihood of an individual learning a novel behaviour socially. Individuals are not uniform in their likelihood of using social over personal information (Grüter et al. 2008; Baciadonna et al. 2013), whilst phenotypic factors such as learner age (Thornton and Malapert 2009), rank (Kendal et al. 2015) and personality (Carter et al. 2014) can inhibit the acquisition, application, and exploitation of social information by learners (Carter et al. 2016). In addition, different age-sex classes can have varying tendencies to monitor other individuals (Lonsdorf 2005) or differ in their gaze attention towards different sexes (van de Waal et al. 2010; Renevey et al. 2013). It therefore seems likely our results are directly applicable to a range of social systems and that our model can be used to make predictions about the processes promoting or inhibiting the emergence of animal cultures.

When transmission probability was very low (e.g., complex/infrequent behaviours or low prestige of demonstrators) we observed similar proportions of networks adopting an invention across homogenous and heterogeneous populations, highlighting that difficult-to-learn behaviours can reduce diffusion performance generally, independent of the attributes of the individuals. Generally, transmission probability needed to be relatively high to also observe little differentiation between homogeneous and heterogeneous networks. This is likely explained by the presence of heterogeneity yielding a number of individuals with low propensities to learn, such that transmission probability must be high (e.g., simple/frequent behaviours or high prestige of demonstrators) for these low propensity individuals to learn as readily as higher propensity individuals.

Social learning may be less likely when tasks or behaviours are complex, for example, vervet monkeys (*Chlorocebus pygerythrus*) were shown to perform well at a one-step foraging tasks (van de Waal et al. 2013), yet failed to solve a two-step task despite having access to social information (van de Waal and Bshary 2011). By including transmission probability in the probabilistic procedure together with variables for random stochasticity and individual propensities for social learning, we account for all sources of variation across a range of scenarios. For example, if a naïve individual has a high propensity to learn whilst transmission probability is high then our procedure is mimicking scenarios where demonstrator prestige and social bond strength are high, behaviour complexity is low and/or performed frequently, and the naïve individual has a high propensity to monitor the actions of other individuals, acquire and process the novel information, and subsequently perform the behaviour effectively. Although future research may benefit from disentangling these factors explicitly (Perry et al. 2021), especially the distinct elements of the social learning process (Carter et al. 2016), it will likely demonstrate similar results to our own – that increasing complexity and heterogeneity diminish the overall likelihood of inventions establishing within social groups.

In addition to learner heterogeneity, homophily in learners similarly hindered information transmission and establishment, but only found when transmission probability was ≥ 20% and ≤ 30%. Figure 4 also shows several examples of the lower quartiles, whiskers, and outliers of homophilic allocations being close to or equal to zero, even when transmission probability is above 20%, this highlights that homophily was more likely to result in little to no diffusion than random distributions. Diffusion models have shown that homophilic distributions can enhance the initial diffusion of information or contagion in a population (Jackson and López-Pintado 2013), i.e., via rapid diffusion between similar phenotypes; however, our results are the first to demonstrate that attribute distributions can have a negative effect on the likelihood of an entire population adopting a behaviour or trait, regardless of population size or network characteristics. Thus, overlooking homophily should also result in anticonservative estimates of the likelihood of inventions establishing in animal groups, obscuring our understanding of animal cultures.

Our homophily procedure also highlighted that different networks are more or less constrained in their ability to exhibit assortative mixtures for a given attribute (see table S1), with the high-density baboon grooming and mixed birds networks producing low assortativity values of 0.02 and 0.06 respectively (average of 50 runs). Despite this, however, we still found significant differences in diffusion performance between random and homophilic allocations across all of the animal groups we tested. The magnitude of this difference may be higher in species whose networks demonstrate higher levels of assortativity, such as Guianan squirrel monkey (*Saimiri sciureus*) groups (Pasquaretta et al. 2014). Future research would benefit from adapting our homophily procedure to explicitly control the level of homophily within each network alongside the extent of heterogeneity in phenotypic traits. This would allow researchers to evaluate the extent of diffusion as a function of the interaction between varying levels of heterogeneity, homophily, and transmission probability.

Typically, the study of how network structure affects diffusion has explored the role of degree distribution (Newman 2002; Jackson and López-Pintado 2013), with the distance between individuals and the number and strength of social connections having been shown to have a negative effect on diffusion speed, fidelity, and robustness (Voelkl and Noë 2010). In our case, the likelihood of inventions establishing did not vary according to substantial differences in group size and moderate variability in network density and clustering coefficients (table S1). In experimental honeybee colonies, contagions can get trapped within a few nodes (i.e., bottlenecking) when networks exhibit high levels of clustering and low levels of robustness (Naug 2008). In the case of our model, if an informed individual had a single connection, then diffusion was likely to be slower than when demonstrators had multiple naïve individuals paying attention concurrently, thus information was likely to bottleneck if an informed demonstrator’s sole connection was to a naïve individual with a low propensity for social learning. However, all of the animal networks we used had moderate density and low global efficiency (i.e., most individuals had several connections), reducing the incidence of bottlenecking. Given the taxonomic breadth of the networks we used, it seems likely that several vertebrate species have network structures that should promote the establishment of inventions. As other species/groups may demonstrate slightly higher global efficiencies than the networks we used here (e.g., (Pasquaretta et al. 2014)), we suggest that future work expands our scope to a wider range of animal groups to confirm whether heterogeneity and homophily are invariably more important than network structure for determining the establishment of animal cultures.

To create a well-functioning and interpretable model it is vital to make some simplifications to certain processes (Grimm and Railsback 2012; Ekanayake-Weber and Swedell 2021). In our model, if the social learning conditions were met, then an individual had an opportunity to learn from an informed demonstrator. Although this condition simplifies the complexities of social learning, it allowed the transmission process to encapsulate several sources of variation, including stochastic processes, task complexity, and demonstrator prestige which animal culture models have not typically included thus far. Our model therefore placed a strong onus on the learner's attributes in determining the diffusion process, thus if the naïve individuals exhibited predominantly low propensities to learn, then diffusion processes were likely to halt unless transmission probability was high. The specific positioning of the seed in different networks exhibiting varying levels of heterogeneity and assortativity requires more thorough investigation (Perry et al. 2021), our model can be used to address these questions and has the option to systematically vary the prestige of the seed. Our results also indicate, however, that the attributes of the seed's neighbours could be just as vital to consider and experimentally manipulate, especially if networks exhibit low clustering and density, but high efficiency.

Given that the spread of inventions relies upon transmission between socially-linked group members, our model can also be used to devise predictions about how network structure, individual heterogeneity, and homophily combine to affect the spread of other types of information or diseases. For instance, the extent of predator detection in groups can rely on social information transfer, but the age, rank, sex, or personality of the initial detector (i.e., the seed) and their relationships with local individuals may combine to determine how rapidly and far-reaching this threat information spreads (LaBarge et al. 2021). Similarly, theoretical models have shown that network structure influences the speed and likelihood of diseases infecting entire groups, but are yet to explore the role of individual heterogeneity and homophily in the latter 'establishment' step (Evans et al. 2021). The individual heterogeneity variables in our model can be easily updated to other phenotypic information besides *propensity for social learning* (e.g., specific personality traits or susceptibility to infection), allowing researchers to test new theories across a range of fields.

In summary, we identified clear negative effects of learner heterogeneity and homophily on the likelihood of cultures emerging across a range of animal groups with networks exhibiting varying topographies and sizes. Generally, both heterogeneity and homophily reduced the extent of information diffusion in the middle of the transmission probability range. Given the similarities in results, despite varied taxa, we believe our results demonstrate that the use of homogeneous actors and random attribute distributions in networked agent-based models may produce anticonservative estimates regarding the establishment of inventions. As there is vast evidence demonstrating that individual heterogeneity can effect the structure, behaviour, and function of animal groups (Jolles et al. 2020), heterogeneity and homophily should also be important considerations in any study exploring the factors determining whether inventions become established in groups and populations. Our model allows for network data to be input from a range of systems whilst including and explicitly manipulating both individual heterogeneity and homophily. As a result, researchers can explore hypotheses and make predictions about social learning processes and the circumstances under which culture may or may not emerge in a wide range of biological systems.

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